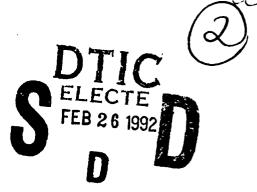
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COLLATERAL BEHAVIORS AND RHYTHMIC PATTERNS IN DOLPHIN ECHOLOCATION

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INTRODUCTION

An echolocating dolphin is not a stationary sonar device; it is a highly mobile actively scanning, living, breathing organism. As the animal echolocates, it is also swimming. In addition, it may be swinging its head to and fro, rolling on one side, opening its mouth, or engaging in any number of other behaviors, overt or subtle. It may even be moving its sound beam internally, within the forehead.

These movement patterns have, in general, been mentioned only in passing in the literature. In fact, most echolocation studies have specifically sought to restrain the animal, usually by having it station on a bite plate or chin cup, so the sound source could be more precisely located.

We believe, however, that such collateral behaviors are a vital component of echolocation. Furthermore, the rhythms imposed by its movement patterns may provide the animal with a means of structuring the sound stream, of dividing it into analyzable segments, somewhat as we use the rhythms of our breath stream to impose patterns of stress and intonation in our speech.

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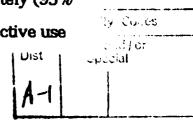
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One reason for believing that various collateral behaviors may be important in dolphin echolocation is that the sound beam is highly structured. The echolocation clicks are short duration (< 200 As), broadband pulses, emitted at repetition rates rangine from less than 1 Hz to more than 600 Hz. Sound is produced within the forehead, probabably via structures called the dorsal bursae (Cranford, personal communication), and is projected outward through the fatty melon in a tightly focused emission beam. The central line of the beam is along the longitudinal axis of the animal, at an angle about 5° above the plane of the teeth (Au et al., 1986). Amplitude is greatest at the center and then drops off rapidly, with a 3-dB beamwidth of about 10° in both the horizontal vertical meridians (Au et al., 1986). Highest frequencies also form a very narrow, central beam, with lower frequencies becoming less and less directional (Norris et al., 1961; Evans et al., 1964). Sound reception is similarly structured into a "cone of reception" (Au and Moore, 1984).

The structured nature of the outgoing beam means that any movements on the part of the dolphin should modulate the amplitude and frequency of the sound at the target and hence modulate the signal the animal receives back. Thus, various motor behaviors could serve to play the sound beam across an object of interest, somewhat as we might explore an unfamiliar object by running our fingers over its surface.

In fact, there may be some interesting parallels between echolocation and what pyschologist James J. Gibson (1962) calls "active touch." Echolocation, like Gibson's active touch, is truly "an exploratory sense rather than a merely receptive sense" (p.477). In a study of tactile pattern discrimination, Gibson found that people could much more accurately (95% vs. 49% correct) match novel objects if they were allowed to make active use

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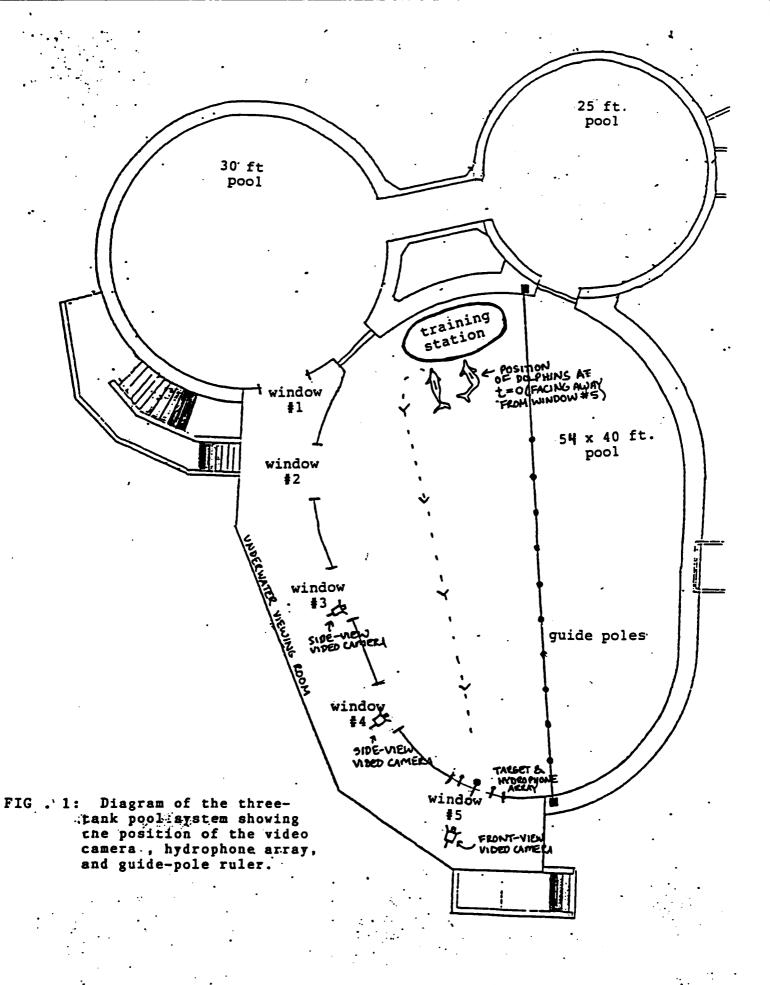
of their hands in exploring an object, as opposed to merely having the object placed in their hand. Similarly, an actively scanning dolphin may actually be a more effective echolocater than a restrained one.

MATERIALS AND METHODS

Subjects. The subjects in our study were two male bottlenose dolphins (*Tursiops truncatus*), Echo and Misha. They were seven and eight years old, respectively, at the time of this study, and each weighed approximately 325 pounds. Both were captured in July 1988 in Tampa Bay, Florida and had not participated in research prior to this study.

Procedures. The animal was first blindfolded by means of a soft suction cup over each eye to ensure that it would use its echolocation and then was asked to swim from a training station at one end of a 54-foot pool to perform some task in front of an underwater viewing window at the other end of the tank. (See Fig. 1 and Fig. 2 for experimental setup.) Tasks included: locating a stationary target and touching the target with the rostrum; locating and retrieving a plastic ring, either one floating at the surface or one sinking down through the water column; locating and eating a fish (dead) drifting in the water.

The stationary target consisted of a plastic pool float attached to the end of a metal rod. It was placed one meter out from the side of the tank and one meter below the surface and was always in the same location. The rings were made of plastic tubing taped into a circle of of approximately 9-inch diameter. One ring had only air in it so it would float; for the other ring, we introduced enough water into the tubing to make it sink slowly. Fish were herring and capeplin (previously frozen), the dolphins' usual





target/hydrophone array

food items. The rings and the fish were tossed into the water with a splash, making a sound the dolphin could orient to initially, on some trials; on other trials, they were placed quietly into the water using a long-handled clamp. Rings and fish were introduced in front (closer to the dolphin, farther from the tank wall) of the target; exact position varied some from trial to trial.

Equipment. The dolphins' movements were recorded during trials on two video cameras from windows in the underwater viewing room. A Panasonic OnmiMovie HQ VHS camcorder behind the target window provided a head-on view of the animal as it approached and performed the task. A JVC autofocus color video camera was placed at one of the side windows (#3 or #4, as shown in Fig. 1) to give a lateral view of the dolphin as it swam across the tank. The two cameras were linked into a split-screen image, so both views could be monitored simultaneously, and which was recorded using a Mitsubishi HQ Stereo Cassette Recorder HS-423VC VCR.

A line of ten 10-ft. PVC pipes, set a meter apart from one another and each marked a 10-cm. intervals, was suspended in the water behind (as seen from the side-view camera) the dolphin's swim route (see Fig. 3). This set of "guide poles" served as a sort of giant measuring stick, allowing us to gauge the dolphin's movement towards the target and his depth in the water column. A circular grid system, drawn on clear acetate (see Fig. 4), was placed in front of the target (head-on view) window to help us measure head movement during scanning.

The dolphin's sounds were picked up by an array of four hydrophones: three B&K 8103s, amplified using B&K 2635 charge



FIG. 3: Side view, showing "guide poles," of dolphin as it swims toward target.



FIG. 4: Head-on view, showing circular grid system, of dolphin as it touches target.

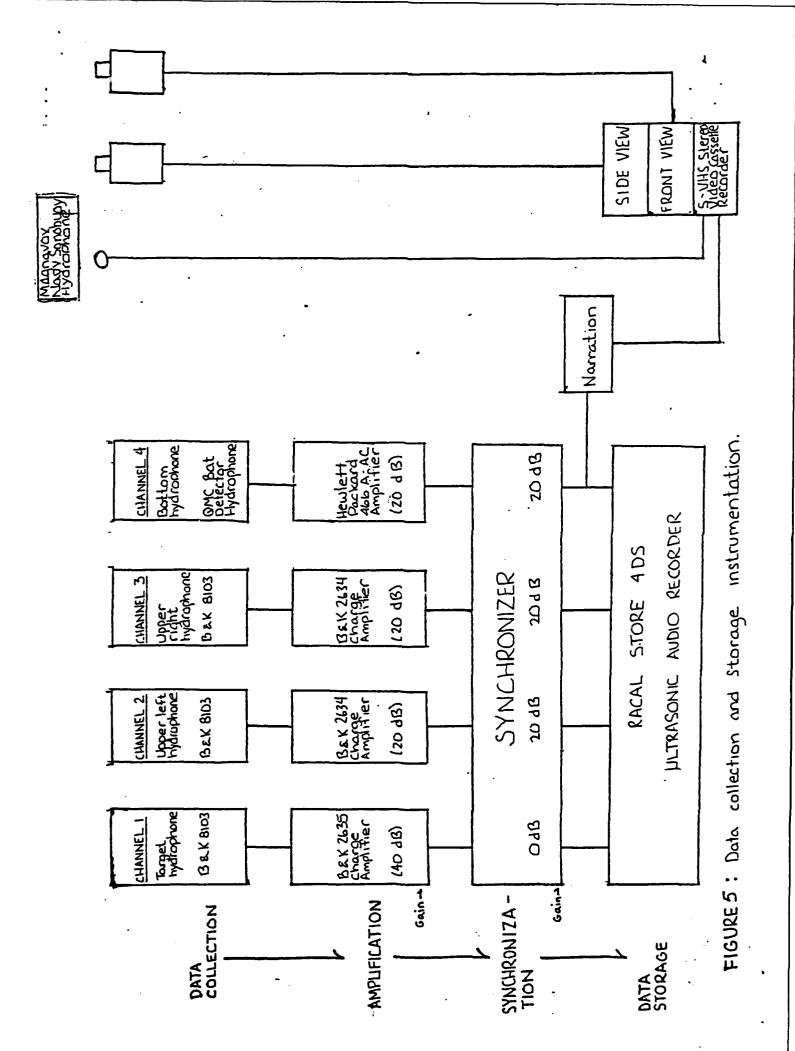
amplifiers, and a QMC Bat Detector hydrophone, amplified with a Hewlett Packard 466 A-AC amplifier (in some sessions either and A.T.I. or and LC-10 was substituted for the Bat Detector hydrophone). (See Fig. 5 for instrumentation setup.) One hydrophone was placed directly on the target itself; the other three were located on a circle around the target hydrophone (see Fig. 6). We used three different array sizes — a radius of 1/2 m. (11 sessions), 3/4 m. (27 sessions) or 1 m. (20 sessions).

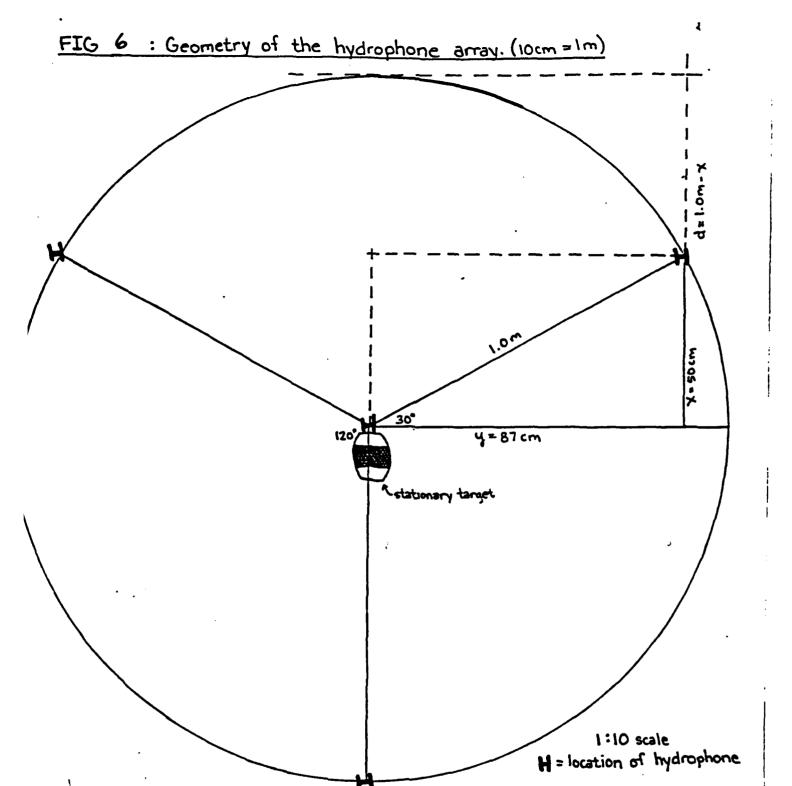
Sounds were recorded on a Racal Store 4DS recorder operating at a tape speed of 60 ips (152.4 cm/s). A specially-built synchronizing device simultaneously activated the video stopwatch and produced a tone recorded on all four channels of the audio tape, allowing us to relate a precise moment in the audio record to the same instant in the video record.

For acoustic analyses the audio tapes were played at 15/16 ips (i.e., at 1/64th the recording speed) into an MCR-214 Recording Oscillograph, equipped with a Model FV-250 Frequency to Voltage Conditioning Module (i.e., it had a frequency mode as well as the usual amplitude mode). This gave us oscillograph printouts of all four channels at once, showing either amplitude or frequency (average peak frequency) over time.

RESULTS AND DISCUSSION

We conducted a total of 58 experimental sessions from July 27, 1989 through December 21, 1989. This resulted in a total of 473 successful two-eyecup trials (not all of which are necessarily analyzable, however, for reasons including poor tank visibility on some occasions or equipment malfunctions). Of these, 213 were target trials, 153 were ring trials and 107 were fish trials. Misha was much slower to accept the eyecups than





1 m array sin 30° = 7 = 50 cm cos 30° = 4 = 87 cm

tan 30° = 1/y = d = 50cm

1/2 m array

y= 43 cm d= 75 cm was Echo, and so we ended up with 149 trials from him as compared to 324 with Echo. We also recorded 67 trials with no eyecups and 197 trials with one eyecup.

Analysis is still underway, so we can't yet report any final results. What follows is a description of the issues we are looking at, along with some preliminary findings.

Swimming Patterns. Here we are looking at various aspects of the dolphin's swimming behavior (bearing in mind the limitations imposed by tank size). For example, does the animal swim in a straight line or does he meander? Does he swim close to the bottom, near the surface, or in mid-water? Is this consistent from trial to trial? Does is differ across tasks? Between animals? When does he surface for a breath? When does he beat his flukes — how fast and how many times? Does his head move up and down in accordance with the fluke beats? How does his swimming motion change as he approaches the target? Is there a set sequence of behaviors he follows for a given task?

In general, both animals tended to take a breath at the outset of their run toward the target, then swim at mid-water level till they reached the target. Both animals generally beat their flukes two or three times at the outset, followed by a brief glide with the body held in a straight line parallel to the tank bottom and the pectoral fins held out like wings. Toward the end of the run, they'd bring their flukes down sharply in a sort of braking maneuver; often they also used both flukes and pecs to steer themselves into position to touch/retrieve/eat the target item. Both animals also quite consistently rolled on one side when they touched the stationary target (and sometimes on ring and fish trials as well). Occasionally, one would swim most of the run on his side, but generally they were upright until they

neared the target.

Because we intermixed several different trial types, however, and the dolphin didn't necessarily know which was coming next, swimming behavior didn't appear to become as stereotyped as it might otherwise. The stationary target task seemed to elicit the most consistent swimming patterns — not surprising since it is the most predictable task, with the target always located in the same position.

We also hope to compare swimming patterns in the two-eyecup trials to some of the trials in which the dolphin was wearing only one eyecup (but echolocated as well as using vision in its uncovered eye) or no eyecups. This would allow us to look for differences according to whether the animal was guided by echolocation only (two eyecups), both echolocation and vision (one eyecup) and vision only (no eyecups).

Head Scanning. Several investigators (e.g., Schevill and Lawrence, 1956; Kellogg, 1960; Norris et al., 1961) have observed that an echolocating dolphin sometimes moves its head back and forth or in subcircular fashion as it closes in on a target. This head scanning behavior appears to occur more often on difficult discrimination tasks and is thought to increase the viewing field, to aid in binaural localization and to increase the effective signal-to-noise ratio (Ralston and Herman, 1988).

Our results thus far support the notion that head scanning is more pronounced on more difficult tasks. In general, the stationary target task elicited less scanning than did the ring retrieval or fish trials (i.e., a moving target). On target runs, the dolphins were more likely to do a quick, short back-and-forth scan about half-way down the pool from the target; ring and fish trials were more likely to bring longer and larger

scanning motions, often in a more circular pattern, much closer in to the object in question. Furthermore, a ring or fish floating at the surface seemed to pose a more difficult problem (presumably because of sound clutter at the water's surface) and hence elicit more head scanning than did one drifting down through the water column.

Further analyses will be aimed at quantifying various aspects of this scanning behavior — how much and in what patterns does he move his head, and how far is he from the target when he scans?

Mouth or Jaw Movements. In the course of the study we noted that the animal sometimes opened its mouth as it swam toward the target. Since the dolphin's sound reception system, at least for high-frequency echolocation sounds, seems to involve the fat-filled mandibular canal (Norris, 1964; Bullock et al., 1968; Brill, 1988), this behavior could actually be a listening technque — and one that could be particularly useful if what you're after is a fish that you want to catch in your mouth. Given the shape of the dolphin's jaw, it could even serve as a sort of megaphone for the incoming sound. We hope to specify, among other things,the circumstances under which this behavior occurs and whether the animal is producing sound at the same time.

Active Listening. A number of authors (e.g., Au, 1990; Awbrey, 1990) have pointed to dolphins' keen hearing ability and suggested that probably get a great deal of information simply by listening — or what has variously been called "passive acoustics," "passive sonar" and "passive hearing," among other things — without generating any sound of their own. Such active listening behavior may be far more important than we've realized. Echolocation is an energetic activity, probably involving considerable wear

and tear on what are surely vital tissues, and dolphins may use it as economically as possible.

Our dolphins apparently didn't do any trials in complete silence when blindfolded; they did, however, sometimes "shut off" their sound for periods as long as one or two seconds in a roughly eight-second run, while proceeding quite accurately towards the target object. On some occasions they even showed head scanning behavior during such silent running. This seemed to occur most often on trials where the task was to retrieve a sinking ring; the ring may make enough noise as it moves down through the water column that the animal can simply find it on that basis.

Duty Cycle. This is, in part, related to the active listening issue. Here we are interested in such questions as: When does the animal turn on his sound and for how long? How many click trains does he use per trial, and how many clicks per train? When do pauses occur, what is the animal doing and how is he oriented during a pause? (Artur Schnable once said, "The notes I handle no better than many pianists. But the pauses between notes — ah, that is where the art resides!" We suspect something of the art of echolocation may also reside in the pauses.)

Beam Steering. There is some evidence to suggest that dolphins may be able to move the sound beam internally, within the forehead, at a rate as much as five times faster than their head movements (Reznikov, cited in Bullock and Gurevich, 1979; Amundin, unpublished manuscript). Such an ability would be particularly useful for close-range discriminations, where the echo returns too quickly for grosser head scanning movements to be of much use.

Because of time and equipment limitations (and because one of our

animals got sick), we were unable to perform the more clear-cut test of the beam steering hypothesis we had hoped. We are, however, looking for evidence of internal beam steering within the trials we did perform — e.g., evidence of oscillation of the sound beam back and forth while the animal's head is stationary. If possible, we will also look for evidence indicating whether such internal beam movement might involve a steering mechanism (sweeping the beam back and forther, or possible up and down) or a focusing mechanism (essentially narrowing and widening the "aperture" of the beam).

Rhythmic Patterning. What we're looking for here is how modulations of the sound structure — in frequency, amplitude, repetition rate and so on — might correlate with the animal's movement patterns. We believe that the movement patterns of an echolocating dolphin could provide some invaluable clues as to organizational principles or "syntax" of its sound production.

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